

1 Sequential Operations Revealed by Serendipitous Feature Selectivity in
2 Frontal Eye Field

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4 **Abbreviated Title:** FEF feature selectivity and sequential operations

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12 analyzed data; K.A.L. and J.D.S. wrote the paper.

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ABSTRACT

Neurons in macaque frontal eye field contribute to spatial but typically not feature selection during visual search. Using an innovative visual search task, we report a serendipitous discovery that some frontal eye field neurons can develop rapid selectivity for stimulus orientation that is used to guide gaze during a visual search task with pro-saccade and anti-saccade responses. This feature selectivity occurs simultaneously at multiple locations for all objects sharing that feature and coincides with when neurons select the singleton of a search array. This feature selectivity also reveals the distinct, subsequent operation of selecting the endpoint of the saccade in pro-saccade as well as anti-saccade trials. These results demonstrate that target selection preceding saccade preparation is composed of multiple operations. We conjecture that singleton selection indexes the allocation of attention, which can be divided, to conspicuous items. Consequently, endpoint selection indexes the focused allocation of attention to the endpoint of the saccade. These results demonstrate that saccade target selection is not a unitary process.

SIGNIFICANCE STATEMENT

Frontal eye field is well known to contribute to spatial selection for attention and eye movements. We discovered that some frontal eye field neurons can acquire selectivity for stimulus orientation when it guides visual search. The chronometry of neurons with and without feature selectivity reveal distinct operations accomplishing visual search.

KEYWORDS

Attention, learning, memory, habit, prefrontal cortex, salience

68 INTRODUCTION

69 To navigate in and interact with the visual world, primates must locate and identify
70 objects to scrutinize through gaze. To understand how this localization, identification and gaze
71 shifting is performed, we use visual search tasks in which targets for gaze shifts are presented
72 with distracting stimuli. Target stimuli can be distinguished from distractors by some feature or
73 set of features (Wolfe & Utochkin, 2019). Targets are sought through an interplay of
74 localization, identification, and saccade preparation manifest as covert and overt orienting.

75 The frontal eye field (FEF), in prefrontal cortex, is known to support attention and eye
76 movements and the performance of visual search (see Bisley & Mirpour, 2019; Schall, 2015 for
77 review). Neurons in FEF respond to visual stimulation, before eye movements, or both (Bruce &
78 Goldberg, 1985; Lowe & Schall, 2018; Schall, 1991). FEF has been conceptualized as a
79 salience or priority map (Bisley, 2011; Fernandes et al., 2014; Thompson & Bichot, 2005),
80 meaning that its responses are related to whether a stimulus is important for attention or gaze
81 shifts regardless of what features make it important (Mohler et al., 1973; Monosov et al., 2010;
82 Ogawa & Komatsu, 2006; Ramkumar et al., 2016; Schall et al., 1995; Zhou & Desimone, 2011).
83 However, FEF is also an ocular motor center (Schall, 2015). Therefore, experimental
84 manipulations are needed to dissociate selection of a stimulus as a conspicuous object,
85 selection of a stimulus as a potential endpoint of a gaze shift, or preparation of a saccade
86 (Matsushima & Tanaka, 2014; Murthy et al., 2001; Sato et al., 2001; Sato & Schall, 2003;
87 Scerra et al., 2019; Thompson et al., 1996; Trageser et al., 2008; c.f. Costello et al., 2013).

88 Our laboratory designed a visual task to dissociate localization of a color singleton from
89 the endpoint of a saccade reporting its location (Sato & Schall, 2003; Schall, 2004). The
90 orientation of a color singleton cued monkeys to produce either a pro-saccade to the singleton
91 or an anti-saccade to the distractor at the opposite location. We have improved the task by
92 making the distractors elongated. This requires monkeys to select on color but respond on
93 shape, resembling classic filtering tasks (Eriksen & Eriksen, 1974; Sperling, 1960; Theeuwes,
94 1992; Treisman & Gelade, 1980). The literature is divided on whether selecting an object and
95 categorizing it are separate, sequential stages (Broadbent, 1971; Hoffman, 1978; Treisman,
96 1988; Wolfe et al., 2015) or objects are selected and categorized in a single step (Bundesen,
97 1990; Logan, 2002). Thus, whether covert and overt orienting processes are comprised of
98 distinct operations or stages remains uncertain.

99 These differing views can be resolved through measurements of neural chronometry
100 (Fig. 1). In the pursuit of this research aim, reward contingencies allowed one monkey to
101 discover a strategy that prioritized the shape of the stimuli. Unexpectedly, some neurons
102 recorded during this task exhibited rapid selectivity for stimulus shape. Here, we compare these
103 findings to a previous report of color selectivity in FEF (Bichot et al., 1996) and characterize the
104 neural chronometry of these FEF neurons. The results provide new evidence that selection of
105 objects and saccade endpoints are distinct operations, both accomplished by visually
106 responsive FEF neurons. The time course of this feature selectivity provides new evidence that
107 visual search is accomplished through sequential operations.

108 METHODS

110 *Subjects*

111 Data from one male macaque monkey (*M. radiata*) was compared to data previously
112 collected from four male macaque monkeys (*M. mulatta*). All procedures were in accordance
113 with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and
114 approved by the Vanderbilt Institutional Animal Care and Use Committee.

115

116 *Visual Search Task*

117 All macaque monkeys performed color singleton visual search tasks. For two monkeys
118 (A, C) the colors of singleton and distractor were constant, giving rise to strong search
119 performance asymmetries (Bichot et al., 1996). For two monkeys (B, Q) the singleton and
120 distractors alternated between red/green or green/red across sessions. New performance and
121 neurophysiology data were collected from another monkey (Da) performing the visual search
122 task with pro- and anti-saccades (Sato & Schall, 2003). The orientation of the singleton cued the
123 pro- or anti-saccade and was presented with elongated distractors. The monkey was trained to
124 fixate a central point whose appearance marked the beginning of the trial. After fixating this
125 point for between 300 and 800 ms, an array of four rectangular stimuli appeared between 3°
126 and 10° eccentricity. One of these stimuli was a color singleton (either red with green distractors
127 or green with red distractors). The color of the singleton and distractors were randomly assigned
128 on a trial by trial basis. All stimuli had an area of 1 square degree. Singletons could be either
129 vertical (aspect ratio = 4.00) or horizontal (aspect ratio=0.25). Distractors could be either
130 vertical, horizontal, or square (aspect ratio = 1.00). The aspect ratio of the color singleton
131 indicated a response rule. If the singleton was vertical then reward was delivered for a saccade
132 to the singleton (pro-saccade; Fig. 2A). If the singleton was horizontal then reward was
133 delivered for a saccade to the stimulus located opposite to the singleton (anti-saccade). After
134 making the saccade, the monkey was required to fixate the correct stimulus for 400 ms, until the
135 fluid reward was delivered. If the monkey broke fixation or made a saccade to an incorrect
136 location, a 2,000 ms time-out delay occurred.

137 Correct responses were defined by the orientation of the color singleton. Hence, the
138 orientation of the distractors can influence response selection. Consequently, particular
139 combinations of singleton and distractor orientations can cue congruent or incongruent
140 saccades. The distractor opposite the singleton was a correct endpoint on anti-saccade trials,
141 so congruency was operationalized by the relationship of the shape of the singleton and the
142 distractor at the opposite location. If the distractor was vertical, a saccade may be planned
143 toward it. If it was horizontal a saccade may be planned toward the color singleton. If the
144 saccade consistent with the orientation of the opposite distractor corresponded to the saccade
145 cued by the singleton, then the stimulus array was *congruent*. If the singleton and opposite
146 distractor cued saccades in opposite directions, then the stimulus array was *incongruent*. If the
147 opposite stimulus was square, the stimulus array was *neutral*.

148

149 *Data acquisition and analysis*

150 Because all details have been described previously (Cohen et al., 2009; Sato et al.,
151 2001; Schall et al., 1995), they will not be repeated. The following approaches and definitions
152 are particular to this analysis.

153 For averaging across neurons, SDFs were normalized by z-scoring across the full trial
154 and performing a baseline subtraction. That is, the SDFs aligned on array presentation and

155 saccade for each condition were concatenated and the standard deviation of this concatenated
156 vector was calculated. The SDFs for that unit were then divided by that standard deviation.
157 Then, the mean baseline activity, the average value of the SDF in the 300 ms preceding array
158 onset, was subtracted. This method of scaling responses reduces the skewness of the SDF
159 across the population and generates a comparable range of activity across neurons without
160 erroneously scaling neurons with little to no modulation (Lowe & Schall, 2018).

161 Selection times were calculated from the SDFs by subtracting the mean difference
162 during the 300 ms before array onset from the difference between two conditions. Selection
163 times were defined as the earlier of two times (1) the time the difference function exceeds 2
164 standard deviations of the baseline difference and continues on to exceed 6 standard deviations
165 for at least 20 ms continuously or (2) the time the difference function exceeds 2 standard
166 deviations of the baseline difference for at least 50 ms continuously. Visual latency was
167 calculated in a similar fashion where the SDF itself meeting the above criteria as opposed to a
168 difference function. Differences among selection time distributions were assessed with a
169 nonparametric Kruskal-Wallis test for equal medians.

170 Each selection time measure was calculated over all RTs and in groups of trials with
171 shortest and longest RTs based on median split. The magnitude of any difference in selection
172 times across RT groups was compared to the difference in RT across the groups through a two-
173 tailed t-test and associated Bayes factor.

174

175 RESULTS

176 *Performance Results*

177 We begin by introducing a nomenclature used below. Correct saccades to vertical stimuli
178 included pro-saccade trials with congruent, neutral, or incongruent arrays (Pro^{C,N,I}) and
179 congruent anti-saccade trials (Anti^C). We also designate saccades to square stimuli as neutral
180 anti-saccade trials (Anti^N) and saccades to horizontal stimuli as incongruent anti-saccade trials
181 (Anti^I).

182 RT and accuracy both exhibited an influence of response mapping and singleton-
183 distractor congruency (Fig. 2B). As expected, mean RT \pm SEM on all anti-saccade trials ($311 \pm$
184 48 ms) was significantly greater than RT on all pro-saccade trials (240 ± 28 ms) (ANOVA:
185 $F(1,198) = 182.5$, $p < 0.001$). A Bayesian analysis suggested that the data were 2.8×10^{22} times
186 as likely to have been observed in a model including stimulus-response mapping as a factor as
187 compared to a null model. Also, RT on all incongruent trials (304 ± 57 ms) was significantly
188 greater than RT on all neutral trials (282 ± 50 ms), which was significantly greater than RT on all
189 congruent trials (260 ± 45 ms) (ANOVA: $F(2,198) = 20.9$, $p < 0.001$). A Bayesian analysis
190 suggested that the data were 1.7×10^7 times as likely to have been observed in a model
191 including congruency in addition to stimulus-response mapping as compared to a model with
192 stimulus-response mapping alone. Thus, the shape of the distractors influenced the efficiency of
193 visual search and saccade production. A Bayesian analysis suggested no evidence of an
194 interaction; the data were 1.24 times as likely to have been observed in a model with no
195 interaction as compared to a model with an interaction between stimulus-response mapping and
196 congruency.

197 Analyzing the pattern of errors, we discovered that the monkey more commonly shifted
198 gaze to a vertical item than to any other (Fig. 2C). Endpoint errors were significantly more

199 common to vertical stimuli ($80 \pm 12\%$ vertical, $10 \pm 7\%$ square, $11 \pm 7\%$ horizontal; ANOVA:
200 $F(2,117) = 833.92$, $p < 0.001$). A Bayesian analysis suggested that the data were 3.6×10^{65}
201 times as likely to have been observed in a model including shape as a factor as compared to a
202 null model. The preference for vertical stimuli was evident also in the RT (Fig. 2D). RTs were
203 significantly shorter for saccades to vertical (271 ± 38 ms), relative to square (339 ± 49 ms) and
204 horizontal stimuli (394 ± 67 ms) (ANOVA: $F(2,234) = 110.15$, $p < 0.001$) regardless of correct or
205 error trial outcome (ANOVA: interaction $F(2,234) = 0.58$, $p = 0.561$). A Bayesian analysis
206 suggested that the data were 3.8×10^{30} times as likely to have been observed in a model
207 including shape as a factor as compared to a null model. There was also no evidence of an
208 interaction, as the data were 8.3 times as likely to have been observed in a model with only
209 shape and trial outcome as factors as compared to a model with an interaction. The more
210 frequent and faster responses to vertical stimuli indicate that the monkey adopted a strategy of
211 searching for vertical items as opposed to guiding gaze by the stimulus-response rule provided
212 by the singleton. In other words, the monkey divided attention to vertical items in the array
213 rather than focusing attention on the singleton that cued the stimulus-response rule.
214 Serendipitously, the short-cut used by the monkey revealed new properties of feature and
215 spatial processing supporting visual search with arbitrary stimulus-response mapping.

216 217 *Shape Selectivity in FEF*

218 Based on previous observations during color singleton search with fixed target and
219 distractor color assignments (Bichot et al. 1996), we tested whether the predisposition for
220 vertical stimuli was associated with altered stimulus feature processing by FEF neurons. FEF is
221 comprised of a diversity of neurons with visual, visuomovement, movement, and other patterns
222 of modulation (Lowe & Schall 2018). The sample of neurons analyzed for this report consisted
223 entirely of visually responsive neurons. This is important to understand because we will describe
224 a pattern of modulation that is related to saccade production but is distinct from the saccade
225 preparation accomplished by movement neurons.

226 Responses to the different stimulus shapes was assessed when they were irrelevant
227 distractors, i.e., not the color singleton nor the endpoint of an anti-saccade or error saccade.
228 Responses to vertical, square, and horizontal irrelevant distractors from two example neurons
229 are shown in Fig. 3A. Both neurons responded more to a vertical than to any other item in the
230 RF. The time at which this difference between responses to vertical and non-vertical stimuli was
231 defined as *feature selection time* (FST). For neuron 1, FST occurred 136 ms after array
232 presentation, 41 ms after the initial transient. FST for neuron 2 occurred 95 ms after array
233 presentation, only 8 ms after the visual transient. These representative neurons exemplify two
234 other distinctive properties. Whereas neuron 1 showed graded selectivity (vertical > square >
235 horizontal), neuron 2 showed categorical selectivity (vertical > square = horizontal) (e.g., Ferrera
236 et al., 2009). The average responses to vertical, square, and horizontal objects for the feature
237 selective neurons is shown in Fig. 3B. The mean \pm SEM FST was 130 ± 30 ms (mode = 134
238 ms; Table 1).

239 In monkeys performing color singleton search with constant target and distractor colors,
240 the color-selective neurons in FEF responded with latencies not less than ~ 60 ms, while non-
241 selective neurons responded with latencies as short as ~ 40 ms (Bichot et al., 1996). We
242 compared the current results to those data (Fig. 4). For each neuron, an ANOVA was performed

243 on the SDF values during the first 25 ms (corresponding to the interval used by Bichot et al.
244 (1996)) or 100 ms after the visual transient. Of 124 neurons sampled, 13% showed shape
245 selectivity in the first 25 ms and 24% in the first 100 ms. As observed previously, neurons with
246 shape selectivity were not the earliest to respond. The earliest visual response of shape
247 selective neurons was 66 ms (median 95 ms; mode 89 ms), later than the two earliest visual
248 responses from non-shape selective neurons 52 and 58 ms). Combined across the two studies,
249 the results show that neither shape nor color information arrives in FEF via the fastest visual
250 pathway and indicate that the training conditions of the present study created the same feature
251 selective state.

252

253 *Relation of Feature Selection to Spatial Selection*

254 The serendipitous discovery of orientation sensitivity in FEF offered an opportunity to
255 relate these observations to previous findings (Thompson et al., 1996; Murthy et al., 2001; Sato
256 & Schall, 2003; Schall 2004). We performed the following sequence of analyses. To report the
257 findings most clearly and concisely, we introduce a nomenclature to distinguish the categories
258 of neurons, the types of trials and the timing measures. First, as previously, we distinguish
259 singleton selection time (SST) from saccade endpoint selection time (EST). Second, we
260 distinguish whether measures were obtained in correct or error trials with left subscript, e.g.,
261 $_{\text{Corr}}\text{EST}$ and $_{\text{Err}}\text{EST}$. Third, we distinguish whether measures were obtained in pro- or anti-
262 saccade trials with right subscript, e.g., $_{\text{Corr}}\text{EST}_{\text{Pro}}$ and $_{\text{Corr}}\text{EST}_{\text{Anti}}$. Finally, we distinguish whether
263 the measure was obtained in trials with congruent, incongruent, or neutral search arrays with
264 right superscript, e.g., $_{\text{Corr}}\text{EST}^{\text{C},\text{I}}_{\text{Pro}}$ and $_{\text{Corr}}\text{EST}^{\text{C},\text{I}}_{\text{Anti}}$. The absence of a particular superscript or
265 subscript implies that the measure was obtained over all possible groups. The authors
266 appreciate the complexity of this nomenclature, which is in keeping with that of more mature
267 scientific fields such as chemistry, molecular biology, and physics that require non-intuitive but
268 detailed nomenclatures and symbols.

269 In the first analysis, responses during pro- and anti-saccade trials were assessed for the
270 feature selective and the non-feature selective neurons to identify SST and EST as measured
271 previously (Sato & Schall, 2003) (Fig. 5A). In pro-saccade trials, the average response became
272 greater when the singleton was in the RF relative to when it was opposite the RF, replicating
273 Sato & Schall (2003) and numerous other studies describing target selection in FEF during
274 search (e.g., Bichot et al., 2015; Buschman & Miller, 2007; Glaser et al., 2016; Keller et al.,
275 2008; McPeck, 2006; Mirpour et al., 2019; Monosov et al., 2010; Monosov & Thompson, 2009;
276 Phillips & Segraves, 2009; Pouget et al., 2009; Scerra et al., 2019; Schall et al., 1995; Schall &
277 Hanes, 1993; Thompson et al., 1996; Wardak et al., 2006; Zhou & Desimone, 2011).
278 Conversely, in anti-saccade trials, the average response across the sample of feature selective
279 neurons became greater when the endpoint of the saccade was in the RF relative to when the
280 singleton was in the RF. Similar results were found for the non-feature-selective neurons (Fig.
281 5B).

282 These results generally replicate previous observations (Sato & Schall, 2003); however,
283 the absence of SST during anti-saccade trials was unexpected. The monkey's performance
284 strategy resulted in low accuracy for Anti^N and Anti^I trials. Hence, the absence of SST_{Anti} is
285 consistent with a failure to focus attention on the singleton appropriately. Further, the aspect
286 ratio of the stimuli used in this study was greater than that used by Sato & Schall and so was

287 more easily discriminable from central fixation. However, when RTs were longer, due either to
288 more deliberate focusing of attention on the singleton or overall slowing of processing, SST
289 preceded EST during anti-saccade trials (Fig. 6). Therefore, the overall pattern of neural
290 modulation observed in FEF is consistent with the performance data indicating that the monkey
291 divides attention among vertical items, sacrificing accuracy for speed.

292 Across the sample of feature selective neurons, SST measured in pro-saccade trials
293 ($_{\text{Corr}}\text{SST}_{\text{Pro}}$) preceded EST measured in anti-saccade trials ($_{\text{Corr}}\text{EST}_{\text{Anti}}$). Average values for these
294 and all subsequent temporal indices \pm SEM are found in Table 1. Statistical tests on all pairs of
295 distributions are found in Table 2.

296 Having established that these relationships replicate previous observations (Sato &
297 Schall, 2003), we can now explore the relationship of the new measure FST to SST and EST
298 measured in the different types of trials. FST was not significantly different than $_{\text{Corr}}\text{SST}_{\text{Pro}}$. In
299 contrast, FST was significantly earlier than $_{\text{Corr}}\text{EST}_{\text{Anti}}$.

300 The simultaneity of FST with $_{\text{Corr}}\text{SST}_{\text{Pro}}$ entails that they index a common process. If so,
301 then FST can inherit the interpretation of SST. Accordingly, we conjecture that FST indexes the
302 process of stimulus selection through attention allocation and not saccade endpoint selection.

303 The second analysis assessed how feature selection was related to spatial selection of
304 locations other than the singleton or saccade endpoint. This was accomplished by contrasting
305 responses of feature-selective neurons to fixated and non-fixated stimuli. Fig. 7A compares the
306 activity of the two example neurons and of the sample of feature-selective neurons to vertical
307 distractors in the RF that were not fixated, activity preceding correct pro-saccades to the vertical
308 singleton in the RF, and activity when unchosen square or horizontal distractors were in the RF.
309 Responses were greater when the vertical color singleton in the RF attracted a gaze shift
310 relative to when a vertical distractor in the RF was not fixated, replicating the well-known
311 enhancement effect (Goldberg & Bushnell, 1981). By comparing discharge rates when an
312 unfixated, irrelevant vertical distractor was in the RF and when the fixated vertical color
313 singleton was in the RF, we measured *endpoint selection time* for pro-saccades ($_{\text{Corr}}\text{EST}_{\text{Pro}}$).

314 The time $_{\text{Corr}}\text{EST}_{\text{Pro}}$ identifies when the endpoint of the upcoming pro-saccade is
315 specified by feature-selective neurons. This is a new measure. It is distinct from EST defined by
316 Sato and Schall (2003), or $_{\text{Corr}}\text{EST}_{\text{Anti}}$ described above because it was not calculated from anti-
317 saccade trials. Across the sample of feature selective neurons, $_{\text{Corr}}\text{EST}_{\text{Pro}}$ was significantly later
318 than FST and $_{\text{Corr}}\text{SST}_{\text{Pro}}$, but was not different from $_{\text{Corr}}\text{EST}_{\text{Anti}}$.

319 The third analysis tested whether $_{\text{Corr}}\text{EST}_{\text{Pro}}$ was due only to the difference in color
320 between the fixated and unfixated vertical items. This was accomplished by contrasting
321 responses when an incorrect saccade was made to a vertical distractor in the RF relative to the
322 un-fixated vertical distractor (Fig. 7B). The response to the fixated vertical distractor was greater
323 than the response to the un-fixated vertical distractor. This replicates multiple previous findings
324 that saccade endpoint errors during visual search arise when FEF neurons treated a distractor
325 as if it were the target (Heitz et al., 2010; Reppert et al., 2018; Thompson et al., 2005). We
326 identify the time when this occurs as *endpoint selection time* for errors ($_{\text{Err}}\text{EST}$). Across the
327 sample of feature selective neurons, $_{\text{Err}}\text{EST}$ was significantly later than FST and trended toward
328 being later than $_{\text{Corr}}\text{SST}_{\text{Pro}}$, but was not different than $_{\text{Corr}}\text{EST}_{\text{Anti}}$ or $_{\text{Corr}}\text{EST}_{\text{Pro}}$.

329 The fourth analysis tested whether the responses of feature-selective neurons varied
330 across trial context. This was accomplished by comparing the responses observed with correct

331 anti-saccades to the vertical item and responses to irrelevant vertical and non-vertical
332 distractors (Fig. 7C). This analysis compared only items of the same color. Both example
333 neurons produced most activity associated with fixated vertical stimuli in the RF relative to un-
334 fixated vertical distractors, and least activity with square or horizontal distractors in the RF.
335 Across the sample of feature selective neurons, the *endpoint selection time for congruent anti-*
336 *trials* ($\text{CorrEST}_{\text{Anti}}^{\text{C}}$) was significantly later than FST but was not different than $\text{CorrSST}_{\text{Pro}}$,
337 $\text{CorrEST}_{\text{Anti}}$, $\text{CorrEST}_{\text{Pro}}$, or ErrEST .

338 These analyses assess the temporal aspects of attention allocation and endpoint
339 selection. Fig. 7 shows three conditions in which vertical items were fixated: correct Pro trials,
340 incorrect saccades to vertical items, and correct Anti^C trials. These were used to identify
341 $\text{CorrEST}_{\text{Pro}}$, ErrEST , and $\text{CorrEST}_{\text{Anti}}^{\text{C}}$, respectively. In a fifth analyses, the magnitude of response in
342 three conditions were compared at three time windows: 100 to 150 ms after array onset (around
343 the time of FST and $\text{CorrSST}_{\text{Pro}}$), 150 to 200 ms after array onset (around the time of EST), and -
344 25 to 25 ms from saccade initiation (Fig. 8). The magnitude of the responses did not differ in the
345 early visual time window ($F(2,87) = 0.022$, $p = 0.9774$), the late visual time window ($F(2,87) =$
346 0.077 , $p = 0.9263$), or around the saccade ($F(2,87) = 0.106$, $p = 0.8994$). In short, responses
347 were identical if a saccade was made toward a vertical item in the RF, regardless of context or
348 whether such a saccade was correct or incorrect.

349

350 *Variation of Modulation Times in Relation to RT*

351 Previous research using this task distinguished neurons by measuring whether SST and
352 EST were synchronized on array presentation or varied with RT (Sato & Schall, 2003; Schall
353 2004). We performed the same analysis for these data, calculating FST, $\text{CorrSST}_{\text{Pro}}$, $\text{CorrEST}_{\text{Anti}}$,
354 $\text{CorrEST}_{\text{Pro}}$, ErrEST , and $\text{CorrEST}_{\text{Anti}}^{\text{C}}$ in the fastest and slowest 50% of trials. The difference in
355 selection times divided by the interquartile range of the RTs could range between 0.0
356 (synchronized on array presentation) to 1.0 (synchronized on saccade initiation).

357 The proportion of RT accounted for by variation in selection times are shown in Fig. 9.
358 We found that this proportion was not different than 0.0 for FST ($t(13) = -0.49$, $p = 0.683$) or
359 $\text{CorrSST}_{\text{Pro}}$ ($t(18) = 0.91$, $p = 0.377$). In terms of Bayes Factors (Rouder et al., 2009) we found
360 moderate evidence that FST (BF = 0.22) and $\text{CorrSST}_{\text{Pro}}$ (BF = 0.28) account for no variability of
361 RT. In other words, the state indexed by FST and $\text{CorrSST}_{\text{Pro}}$ arises at a time synchronized on
362 array presentation.

363 In contrast, variation in all measures of endpoint selection in feature-selective cells
364 accounted for a significant fraction of variation of RT. With strong evidence rejecting the null
365 hypothesis (BF = 24.62), a significant proportion of the variation of RT was accounted for by
366 variation in $\text{CorrEST}_{\text{Anti}}$ ($t(13) = 3.92$, $p = 0.002$). At a moderate level of evidence, a significant
367 proportion of the variation of RT was accounted for by variation in ErrEST ($t(9) = 3.22$, $p = 0.011$,
368 BF = 5.64) and $\text{CorrEST}_{\text{Anti}}^{\text{C}}$ ($t(7) = 2.95$, $p = 0.021$, BF = 3.29). At an anecdotal level of evidence,
369 a significant proportion of the variation of RT also was accounted for by variation of $\text{CorrEST}_{\text{Pro}}$
370 ($t(8) = 2.71$, $p = 0.027$, BF = 2.55).

371 Although the measures of EST account for some RT variability, the average proportion
372 of RT explained across all significant relationships is 24.8%. The additional RT variability will be
373 accounted for by response preparation processes subsequent to EST and not included in these
374 data.

375

376 *Neural Chronometry of Feature and Spatial Selection*

377 The various distinct response modulations reveal a temporal sequence of operations in
378 FEF accomplishing this visual search task (Fig. 10; Table 2). Following array presentation, the
379 first state transition is indexed by the response of visually responsive neurons after a
380 characteristic latency. The next state transition was indexed by FST, which coincided with
381 $_{\text{Corr}}\text{SST}_{\text{Pro}}$. The state indexed by $_{\text{Corr}}\text{SST}_{\text{Pro}}$ has been identified with the allocation of visual
382 attention on the singleton based on its salient visual attribute to encode the stimulus-response
383 rule (Sato & Schall, 2003; Schall 2004). The discovery of feature-selection arising concomitantly
384 with $_{\text{Corr}}\text{SST}_{\text{Pro}}$ reported here suggests that the monkey divided visual attention among the
385 vertical items in the array. The allocation of spatial visual attention to spatially separated,
386 noncontiguous items in a search array has been demonstrated (e.g., Bichot et al., 1999; Dubois
387 et al., 2009). The next state transition was indexed by EST. The state indexed by EST has been
388 identified with the specification of the endpoint of the saccade. Being different in time and
389 relationship with RT, it is a state different from that identified by $_{\text{Corr}}\text{SST}_{\text{Pro}}$ (Sato & Schall, 2003;
390 Schall 2004) and likewise distinct from the presaccadic build-up of movement related neurons
391 (Woodman et al., 2008), which accounts for the remainder of the variation of RT.

392

393 DISCUSSION

394 The present study demonstrates two primary findings: (1) besides color (Bichot et al.,
395 1996), shape selectivity can arise in FEF when strategies commit feature attention and (2) this
396 feature selectivity, which seems associated with divided attention, is functionally distinct from
397 the selection of the saccade endpoint. The first finding may seem at odds with the perspective
398 that FEF selects targets regardless of the feature that identifies a stimulus as that target.
399 However, adaptive performance strategies can explain this anomaly. Strategies are revealed by
400 analyzing the responses made on error trials and RT in all trials. The increased prevalence of
401 error saccades to vertical stimuli and the fastest RT to vertical stimuli reveals a priority for
402 locating vertical stimuli.

403 The results are based on data obtained from a single monkey. Nevertheless, we believe
404 they are reliable and interpretable for the following reasons. First, the observation of feature
405 selectivity in FEF replicates previous findings (Bichot et al. 1996; Peng et al. 2008). A similar
406 predisposition for motion direction has been described in the superior colliculus of monkeys
407 performing a motion discrimination task with fixed stimulus-response mapping (Horwitz et al.,
408 2004). The unexpected but clear robustness of this phenomenon should engender confidence in
409 the replicability of the current observations. Second, the distinction of singleton selection and
410 endpoint selection replicates previous findings (Sato & Schall, 2003; Schall 2004). Such
411 replication should increase confidence in the interpretability of the new findings. Finally, the
412 novel observation of a distinct endpoint selection in pro-saccade trials is statistically robust,
413 conceptually novel, and theoretically important. While we are confident that another monkey
414 could be trained into this state, we judge that effort is better invested in more novel research
415 goals. Indeed, we have discovered that the second monkey, trained without the opportunity to
416 experience the confounds, employs a qualitatively different strategy to perform this task (Lowe
417 et al., 2019).

418

419 *Possible Sources of Feature Selection in FEF*

420 We do not know whether the shape selectivity we observed is intrinsic to FEF, imparted
421 by other prefrontal areas, inherited from earlier visual areas, or manifest from broad
422 associations of stimulus, action, and reward. We consider each hypothesis below.

423 The hypothesis that feature selectivity is intrinsic to FEF runs counter to the framework
424 of FEF as an area that contains a salience or priority map regardless of features defining
425 salience or priority (Thompson & Bichot, 2005). However, some studies have reported
426 differential activity to stimuli defined by features whose identities do not dictate different
427 stimulus-response rules (Ferraina et al., 2000; Peng et al., 2008; Xiao et al., 2006). Mohler et al.
428 1973 reported 6% of FEF neurons (12.5% of those with visual responses) responding differently
429 according to direction of motion or color. Peng and colleagues (2008) found that even during a
430 passive fixation task a quarter of FEF neurons had responses that differed according to the form
431 of the presented stimuli. These differences occurred at most 12 ms after the initial visual
432 transient. This short delay between visual response onset and feature selectivity is consistent
433 with the selectivity for color found previously (Bichot et al. 1996). However, the shape selectivity
434 presented here was not as immediate. This may be due to the nature of the tasks across
435 studies in that there are unbalanced reward contingencies of nonpreferred stimuli in the present
436 study whereas all stimuli were evenly rewarded in the passive fixation and delayed match to
437 sample tasks used by Peng et al. It is notable that the proportions of feature selective neurons
438 found by Peng et al. are similar to those found in the present data, but are fewer than those
439 found by Bichot et al. (1996). This could be due to differences in complexity of the stimuli,
440 nature of the task, or sampling of units.

441 The hypothesis that feature selectivity in FEF can be imparted by another prefrontal area
442 is motivated by the recent description of a ventral prearcuate area (Bichot et al. 2015), which
443 has dense connections with FEF (Huerta et al., 1987). Neurons in this area have differential
444 responses to complex visual stimuli during detection and delayed search tasks, and this feature
445 selectivity preceded the selection of a saccade endpoint (Bichot et al., 2015). However, direct
446 comparison between this and the current study is challenged by differences in experimental
447 design and particular observations. For example, their target item was cued before array
448 presentation and so was held in working memory, but our target item in this study was a long-
449 term memory trace. Also, neurons in the ventral prearcuate area exhibited feature selectivity at
450 approximately the same time as FEF, and the spatial selectivity identified in FEF was earlier
451 than that observed in the present data ($C_{\text{off}}\text{SST}_{\text{Pro}}$). Further research is needed, therefore, to
452 clarify whether FEF receives feature information primarily from this area, or both areas have
453 common inputs and process feature information in parallel.

454 The hypothesis that feature selectivity in FEF is inherited from feature selective
455 responses earlier in the visual stream is motivated by the connections between FEF and
456 effectively all extrastriate visual areas (Schall et al. 1995; Markov et al. 2014). V4 is one likely
457 source because the neurons are selective for color (Schein & Desimone, 1990; Zeki, 1980; Zeki,
458 1973) and shape (Desimone & Schein, 1987; Pasupathy & Connor, 1999). In the previous
459 (Bichot et al. 1996) and current study, neither color nor shape selectivity were carried by the
460 FEF neurons with the shortest visual latencies. This is consistent with color and shape
461 information arriving in relatively longer latency afferents (e.g., Schmolesky et al., 1998).
462 Evidence from simultaneous recordings in FEF and V4 demonstrate an association of visual

463 neurons in FEF with V4 (Gregoriou et al., 2012) and feature selectivity in V4 preceding FEF
464 selective modulation (Zhou & Desimone, 2011). Further research is needed, though, to
465 understand the interplay of feature selectivity and attentional modulation between FEF and
466 extrastriate visual areas (Zhou et al., 2011; see also Monosov et al., 2010).

467 The hypothesis that feature selectivity in FEF is manifestation of the association of
468 strategy and reward is motivated by well-known reports that visual responses in FEF are
469 modulated by reward expectation (Glaser et al., 2016) or magnitude (Ding & Hikosaka, 2006).
470 Parallel modulation is observed broadly in the visuo-motor network (e.g., Griggs et al., 2018;
471 Platt & Glimcher, 1999; Sugrue et al., Newsome, 2004; Yamamoto et al., 2013). In human
472 studies, both reward probability and magnitude have been shown to influence behavior. Della
473 Libera & Chelazzi, (2009) found that by associating meaningless shape stimuli with high, low, or
474 neutral reward in a practice phase resulted in facilitation or interference of response times,
475 depending on task conditions. Similarly, attentional biases emerge when color stimuli are
476 associated with high or low reward, whether or not participants are aware of the stimulus-reward
477 associations (Kiss et al., 2009; Kristjánsson et al., 2010). These associations do not require
478 physical salience as they are present with stimulus configurations that have only reward
479 histories to differentiate stimuli and for which rewarded features are not the basis for selection
480 (Anderson et al., 2011). These findings suggest that stimulus-reward associations can be
481 learned and combined with physical salience to form an integrated priority map (Awh et al.,
482 2012). These reward associations manifest themselves in neural activity (Anderson, 2016). The
483 tail of the caudate is sensitive to learned reward associations (Anderson et al., 2014). Learned
484 value associations are reflected in BOLD signaling in attentional visual areas such as parietal
485 cortex (Anderson et al., 2014) and are reflected in shifts of ERPs indexing attentional selection
486 such as the N2pc (Kiss et al., 2009).

487 In conjunction search FEF neurons respond maximally when the correct saccade target
488 is in the RF (Bichot et al., 2001; Ogawa & Komatsu, 2006) but also show larger responses to a
489 distractor that shares a feature with the correct saccade target than a distractor that shares no
490 features (Bichot et al., 2001). Similarly, FEF neurons respond more when a distractor that was
491 the target on the previous session is in the RF than a distractor that shares no features with the
492 current saccade target. This demonstrates that FEF neurons can differentially respond to
493 features that are remembered to be rewarded even when not presently rewarded. Reward
494 associations, specifically the lack thereof, can also participate in distractor suppression
495 (Cosman et al., 2018). In a search task with salient distractors that “capture” attention
496 (Theeuwes, 1991) two monkeys overcame capture with training and produced equal
497 performance when the color singleton distractor was present or absent. Neurons recorded from
498 those two monkeys showed a reduction in firing rate when the salient distractor was in the RF
499 compared to a non-salient distractor was in the RF. Because the salient distractors were never
500 a saccade target, but were nevertheless distinguishable from the other distractors, responses to
501 them can be more actively and immediately suppressed than the other distractors. Bichot and
502 colleagues (2001) also tested neural responses during a search task with a salient distractor
503 and did not find distractor suppression. However, the monkeys in that study were behaviorally
504 affected by the singleton distractor and thus distractor suppression may not be expected.
505 Further, the neurons analyzed by Bichot and colleagues were movement neurons whereas

506 those analyzed here and by Cosman et al. had visual responses. This difference in neuron type
507 may also explain the differences in results.

508 Interestingly, the third monkey in the study by Cosman and colleagues that was unable
509 to overcome attentional capture was the same monkey Da whose data are reported here.
510 Neurons from this monkey did not show such distractor suppression. Notably, this monkey also
511 had neurons that retained an initial nonspecific visual response whereas monkeys A and C did
512 not have such a response during the color singleton search task. Such an initial visual response
513 is reduced in FEF neurons when stimuli are not saccade targets (or, alternatively, enhanced
514 when they are saccade targets) in both search tasks (Thompson et al., 1997) and in single
515 stimulus presentations (Goldberg & Bushnell, 1981; Mohler & Wurtz, 1976; Schall et al., 1995).
516 In the case of monkeys A and C, the stimuli whose colors were not the target color were never
517 correct saccade targets and can thus be discounted and would have attenuated nonspecific
518 responses to these stimuli, and this attenuation could be complete such that there is no such
519 response. In the case of Da, square and horizontal stimuli were correct saccade endpoints on a
520 subset of anti-saccade trials, thus they are still associated with reward to some degree and thus
521 may require the retaining of the nonspecific visual transient.

522

523 *Processing Operations and Neural Chronometry*

524 We replicated the previous finding of distinct operations mediated by visually responsive
525 neurons selecting a conspicuous stimulus and selecting the endpoint of the saccade (Sato &
526 Schall, 2003). The prior experiment did this by contrasting modulation in pro- and anti-saccade
527 trials. The current experiment did this, innovatively, by contrasting modulation to preferred and
528 non-preferred features and to fixated and non-fixated items among identified neurons exhibiting
529 feature selectivity even for stimuli that should not be and were not selected. Specifically, we
530 demonstrated quantitative differences between two measures of neural modulation: stimulus
531 selection, indexed by FST and $C_{\text{corrSST}_{\text{Pro}}}$, and saccade endpoint selection, indexed by EST. The
532 chronometric distinction between singleton selection and endpoint selection in both pro- and
533 anti-saccade trials and the simultaneity of EST on pro- and anti-saccade trials having very
534 different RT validates the conceptual distinction between these operations. These neural
535 measures index some of the computational operations occupying response time in this task
536 (Donders, 1969).

537 The delay between EST and saccade initiation identifies another operation preceding
538 saccade initiation. This operation has been identified psychologically as response preparation
539 and neurally as the presaccadic build-up of movement related neural activity, which does not
540 occur until information about target items becomes available (Woodman et al., 2008) and is
541 identified with the accumulation of sensory evidence (Purcell et al., 2010, 2012; Servant et al.,
542 2019). The final saccade initiation operation is accomplished by competitive interactions
543 between movement cells (Purcell et al., 2010, 2012). The time required for this competition
544 resolution explains the additional time necessary for anti-saccades compared to pro-saccades.
545 The relationship between stimulus selection, endpoint selection, and saccade preparation has
546 been investigated in monkeys (Juan et al., 2004; Katnani & Gandhi, 2013) and humans (Juan
547 et al., 2008).

548 To verify the existence and elucidate the properties of these distinct operations and
549 stages, and to resolve different explanations for causal manipulations, further research should

550 employ the powerful logic of selective influence in factorial experimental designs (Sternberg,
551 2001; Townsend & Nozawa, 1995) with joint measures of mental and neural chronometry.

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- 806
807

808 **FIGURE LEGENDS**

809 **Figure 1.** Visual search with explicit stimulus-response mapping.

810 (A) Visual search task in which the orientation of a color singleton cues a pro-saccade (vertical),
811 an anti-saccade (horizontal), or no saccade (square). Response times can be subdivided into
812 three states or operations. Array presentation is followed by stimulus encoding and localization
813 (thin line); the conclusion of this operation is indexed by singleton selection time (SST). Next,
814 stimulus-response mapping and selection of the saccade endpoint happens if a pro- or anti-
815 saccade will be produced (thick line); the conclusion of this operation is indexed by endpoint
816 selection time (EST). This operation may not occur when no saccade is made (grayed thick
817 line). Finally, saccade preparation leads to initiation of the saccade which is manifest as the
818 measurement of RT (dotted line).

819 (B) Response time on anti-saccade trials (RT_{Anti}) is systematically longer than that on pro-
820 saccade trials (RT_{Pro}). Measurements of SST and EST provide insight into the operations
821 contributing to the variation of RT. Theoretically, a difference between SST_{Anti} and SST_{Pro} (left)
822 or between EST_{Anti} and EST_{Pro} (right) could explain all (top), some (middle), or none (bottom) of
823 the variation of RT.

824

825 **Figure 2.** Search array configurations and task performance.

826 (A) Visual search with pro-saccade (top) and anti-saccade (bottom) responses based on
827 orientation of color singleton. Distractors could be square or elongated. Because shape of the
828 singleton cues stimulus-response rule, the shape of the distractors may influence the efficiency
829 of stimulus-response mapping via a congruency effect. We operationalized neutral trials as
830 those in which the distractor opposite the singleton was square (left column), congruent trials as
831 those in which the distractor opposite the singleton would cue the same saccade as the
832 singleton (middle column), and incongruent trials as those in which the distractor opposite the
833 singleton cued the opposite saccade (right column). The saccades cued by the singleton
834 (distractor) are indicated as red (green) arrows.

835 (B) Defective RT distributions for pro-saccade (black) and anti-saccade (red) trials with
836 congruent arrays (full saturation), neutral arrays (intermediate saturation), and incongruent
837 arrays (lowest saturation). Saccade latency was longer for anti- relative to pro-saccades, and
838 longer of incongruent relative to neutral and congruent trials.

839 (C) Proportions of error saccades made to each stimulus shape for trials in which at least one
840 distractor was vertical (open).

841 (D) RTs to each stimulus shape for error (filled) and correct (open) trials. Saccades to vertical
842 items were shortest latency.

843

844 **Figure 3** Feature selectivity in FEF.

845 (A) Normalized firing rate for two example neurons that exhibited shape selectivity aligned on
846 stimulus onset. Responses to vertical (green), square (magenta), and horizontal (cyan) stimuli
847 that were irrelevant distractors across correct (blue drop) and error (crossed blue drop) pro- and
848 anti-saccade trials. Trial types are indicated in the color-coded insets. The set of possible stimuli
849 that can appear at a given location are superimposed. The singleton shown at 90° could have
850 appeared at 270° ; likewise, the distractors shown at 270° could have appeared at 90° . Feature
851 selection time (FST) is indicated by the vertical green line.

852 (B) Average normalized firing rate \pm SEM for all feature selective neurons aligned on array
853 presentation (left) and saccade initiation (right). Vertical green line plots the median FST for this
854 population.

855
856 **Figure 4.** Relationship between feature selectivity and visual latency compared for neurons
857 sampled in this study (green) and those reported previously in control monkeys that performed
858 search with variable color assignments (open black circles) and experimental monkeys that
859 performed search with constant color assignments (filled black circles) (Bichot et al. 1996). The
860 probability of the response to the singleton in the receptive field being the same as the response
861 to a distractor in the receptive field during the first 25 ms (A) and 100 ms (B) is plotted as a
862 function of visual response latency. Horizontal lines indicate analysis window. In (B) the dashed
863 portions of the line indicate that the 100 ms analysis window extends beyond the range of the
864 plot. The shaded region indicates nonsignificant probability values greater than 0.05. In the
865 previous study, of the 43 neurons from control monkeys, 39 fell in the nonsignificant area, two
866 responded preferentially to the target, and two responded preferentially to the distractors of the
867 search array field (marked by diagonal lines). In contrast, 21 of 47 neurons recorded from the
868 experimental monkeys exhibited significantly greater initial responses when the singleton fell in
869 the receptive field, and none showed the opposite effect. In the current study, of 124 neurons
870 sampled, 16 showed shape selectivity in the first 25 ms and 30 in the first 100 ms. Example
871 neurons 1 and 2 are identified as N1 and N2.

872
873 **Figure 5.** Singleton and saccade endpoint selection.

874 (A) For the 30 feature selective neurons, average normalized SDF when the singleton appeared
875 in (dark) or opposite (light) the RF during interleaved pro- (top) and anti-saccade (bottom) trials
876 aligned on array presentation (left) and on saccade initiation (right). Insets illustrate the locations
877 and orientations of the singleton and possible horizontal, square, or vertical distractors relative
878 to RF (gray arc) plus the reward earned (drop icon) for each SDF. SST measures when the SDF
879 for the singleton in the RF exceeds the SDF for a distractor in the RF. EST measures when the
880 SDF for the anti-saccade endpoint opposite the RF exceeds the SDF for the singleton in the RF.

881
882 **Figure 6.** Singleton and saccade endpoint selection across response time. Representative
883 neuron illustrating variation of SST and EST for shortest (left) and longest (right) RT (highlighted
884 in inset cumulative RT distributions). In pro-saccade trials, SST does not vary with RT. In anti-
885 saccade trials, SST was manifest in long but not short RT trials, followed by EST. Conventions
886 as in Figure 4.

887
888 **Figure 7.** Distinction of feature selectivity from saccade selection. Normalized firing rates for
889 neuron 1 (1st column) and neuron 2 (2nd column) aligned on array presentation, plus mean
890 normalized SDF \pm SEM of feature selective neurons aligned on array presentation (3rd column)
891 and on saccade initiation (4th column).

892 (A) Activity associated with irrelevant vertical (green), non-vertical (cyan), and the singleton in
893 the RF (black) demonstrate enhancement associated with correct saccade selection, which
894 distinguishes FST from $\text{CorrEST}_{\text{Pro}}$.

895 (B) Activity on pro- and anti-saccade trials associated with irrelevant vertical (green), non-
896 vertical (cyan), and incorrectly selected vertical distractors in the RF (magenta) demonstrate
897 enhancement associated with errant saccade selection, which distinguishes FST from EST_{Err} .
898 (C) Activity on anti-saccade trials associated with irrelevant vertical (green), non-vertical (cyan),
899 and correctly selected vertical distractor in the RF (red) demonstrate enhancement associated
900 with anti-saccade selection, which distinguishes FST from EST_{Anti}^C .

901
902 **Figure 8.** Magnitude of response during saccade selection. Mean normalized SDF \pm SEM of
903 feature selective neurons aligned on array presentation (left) and on saccade initiation (right).
904 Activity associated with correct Pro saccades into the RF (black), incorrectly selected vertical
905 distractors in the RF (magenta), and correct $Anti^C$ saccades into the RF (red) do not differ,
906 showing that this population does not differentiate type of saccade if a saccade is to be made.

907
908 **Figure 9.** Chronometry of feature selection, singleton selection, and endpoint selection in
909 relation to response time.

910 (A) Selection times for faster and slower RT groups plotted as a function of the mean RT of
911 each group. Each line corresponds to one neuron with a measurable selection time in both RT
912 groups. The slope indicates the contribution of each selection time to RT. Inset in top left
913 subplot (FST) illustrates range of possible influences of selection times on RTs. Selection times
914 could be synchronized on array presentation and invariant with respect to RT (0% RT
915 explained) or synchronized on saccade presentation (100% RT explained). Colors as in Fig. 6.
916 Dashed lines indicate measures from non-feature-selective cells.

917 (B) Bayes factors from statistical test of the slopes of each selection time relative to RT. Bayes
918 factors less than 1 (log values less than 0) indicate evidence for the null hypothesis (H_0) that the
919 distribution mean is equal to 0. Bayes factors greater than 1 (logs greater than 0) indicate
920 evidence for the alternate hypothesis (H_1) that the distribution is greater than 0. Levels of
921 evidence defined by the Bayes factor are indicated. Line and color assignments as in Fig 6. We
922 found moderate evidence supporting the hypothesis that FST and SST_{Pro}^{Corr} are synchronized
923 on array presentation and not on saccade initiation. On the other hand, we found strong
924 evidence that EST_{Anti}^{Corr} , anecdotal evidence that EST_{Pro}^{Corr} , and moderate evidence that EST_{Err}
925 and EST_{Anti}^C were not synchronized on array presentation nor saccade initiation.

926
927 **Figure 10.** Distributions of feature selective processes.

928 (A) Diagrams showing sequence of states during pro-saccades (top). The hypothesized
929 spotlight of attention is shown in gray lines and a saccade is indicated by a solid arrow.
930 Cumulative distributions of selection time metrics alongside visual response latency and Pro RT
931 distribution (bottom). The colors are the same as the diagrams and previous figures and labeled
932 above the plot boundary. Line thickness increases as stages become further from array onset
933 and closer to RT.

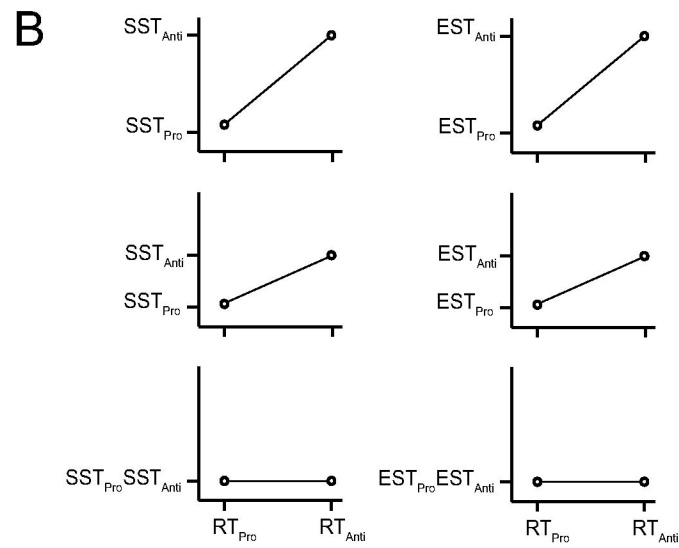
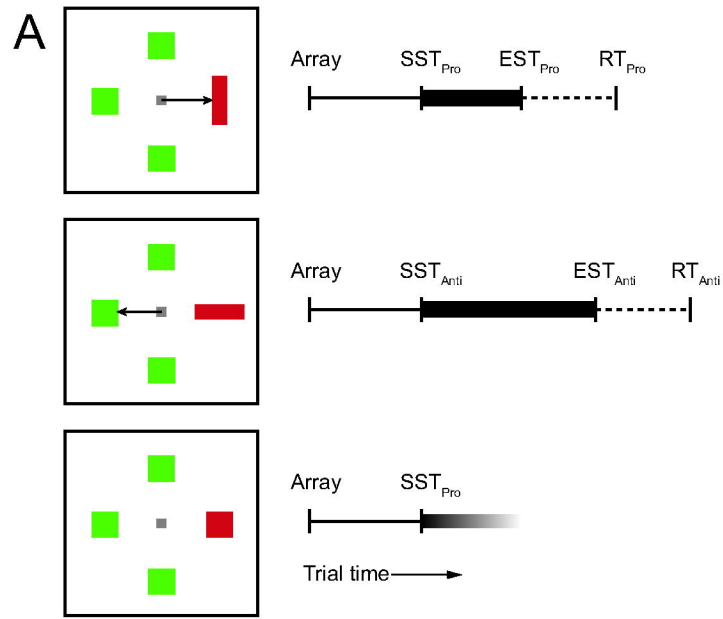
934 (B) Diagrams showing sequence of states during anti-saccades (top) and cumulative
935 distributions of selection time metrics (bottom).

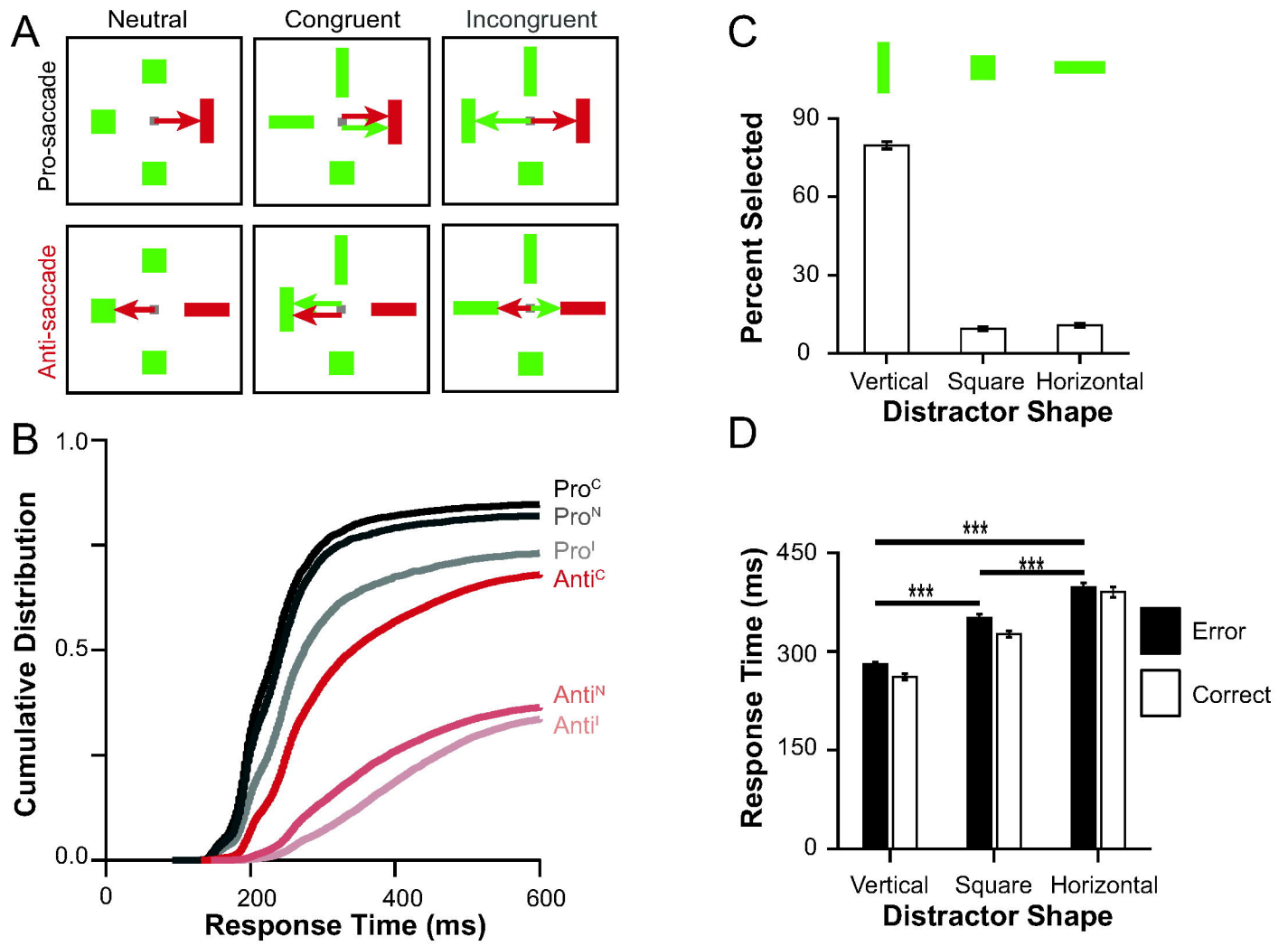
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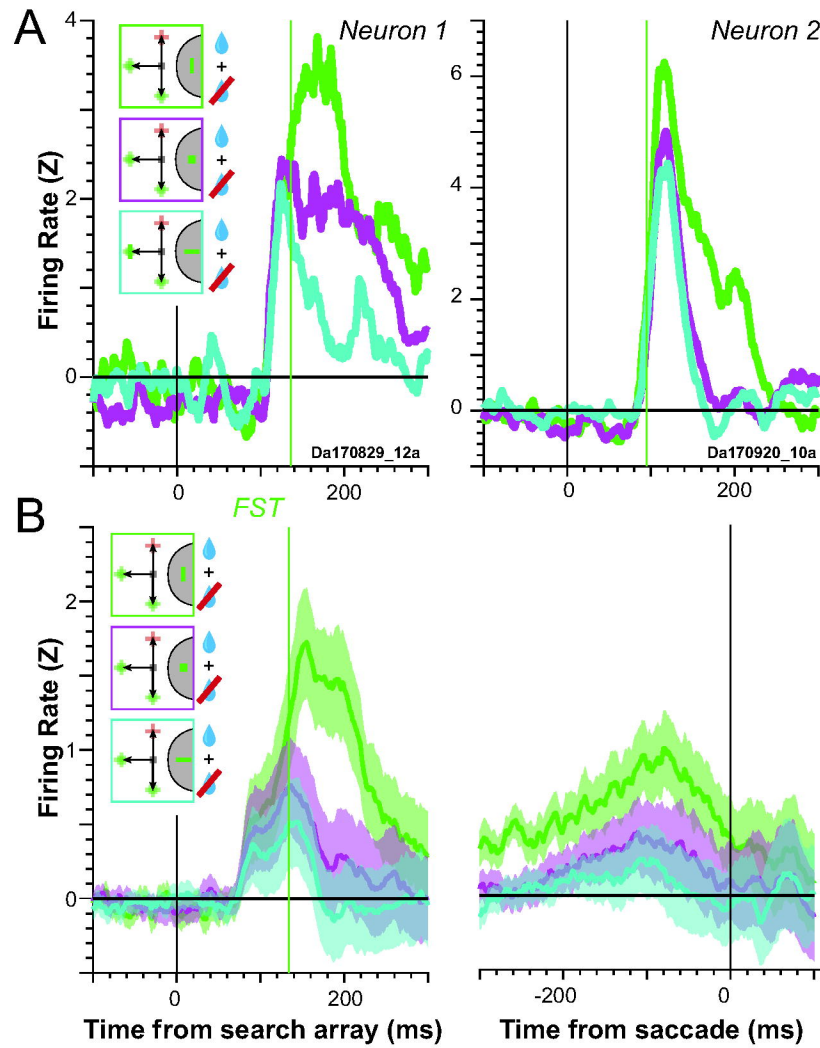
937 TABLE LEGENDS

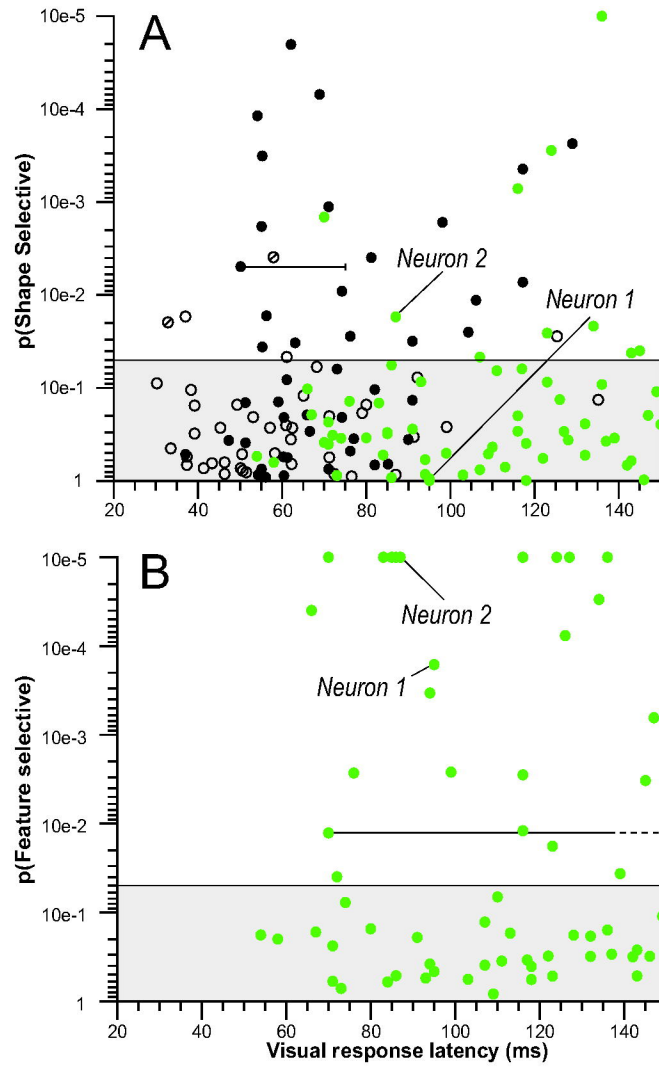
938 **Table 1.** Selection time summary statistics. For each selection time, the table reports the
939 mean value \pm SEM, modal value, probability that variation in selection time over interquartile
940 range of the response times is equal to zero (i.e., the probability that selection time is
941 synchronized to array presentation), and the Bayes factor for whether the change in selection
942 time is synchronized to the change in RT (BF < 0) or not synchronized to the change in RT (BF
943 > 0).

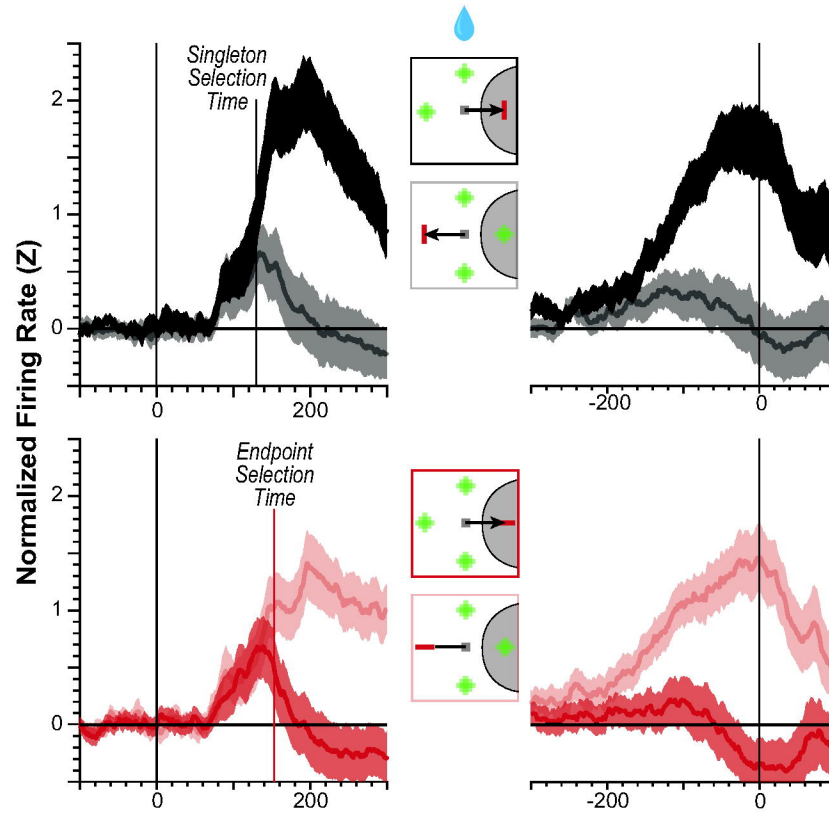
944
945 **Table 2.** Selection time comparisons. The distribution of each selection time was compared to
946 the distribution of each other selection time using a Kruskal-Wallis test. The X^2 value, degrees of
947 freedom, and p value of each pairwise test is shown. Because the tests are symmetric, only the
948 lower diagonal is shown. Values that trend toward significance ($p < 0.10$) are marked with a
949 dagger (†). Values that reach significance ($p < .05$) are marked with an asterisk (*).

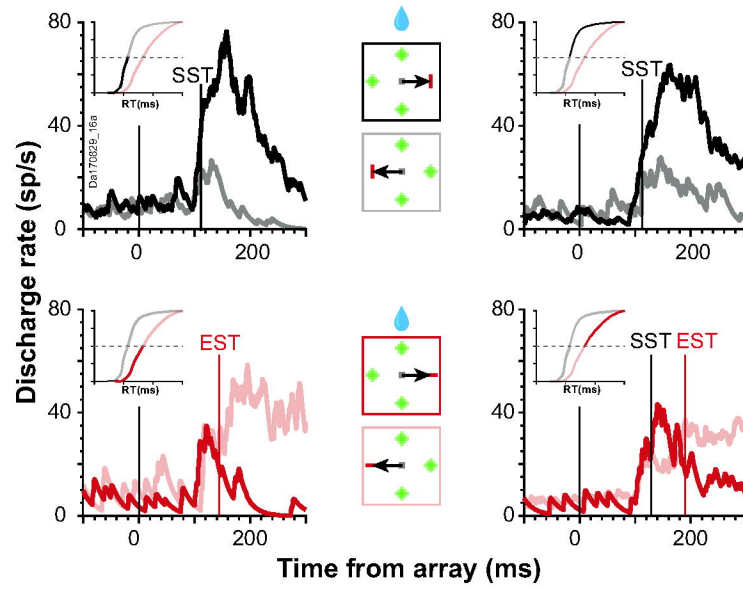


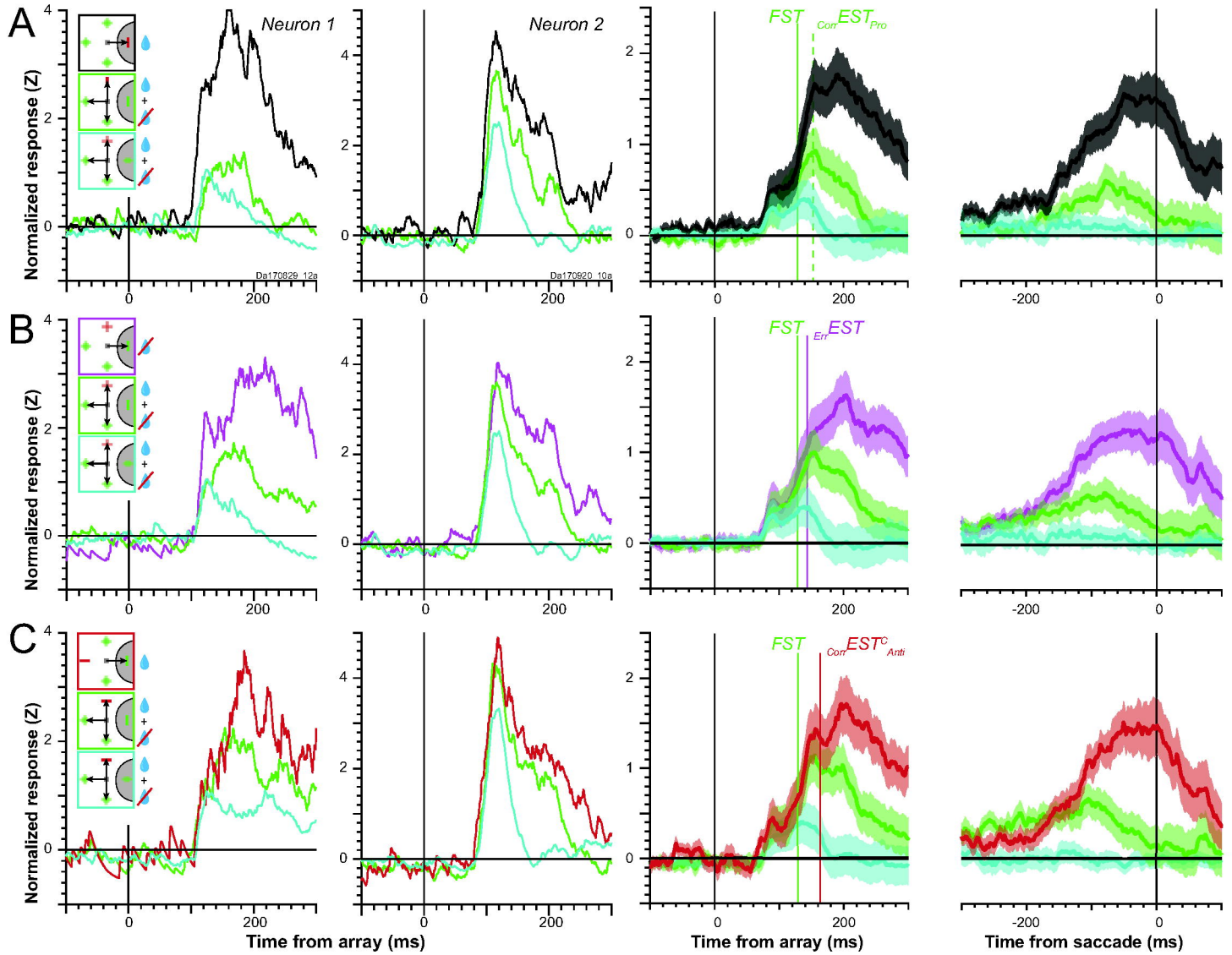


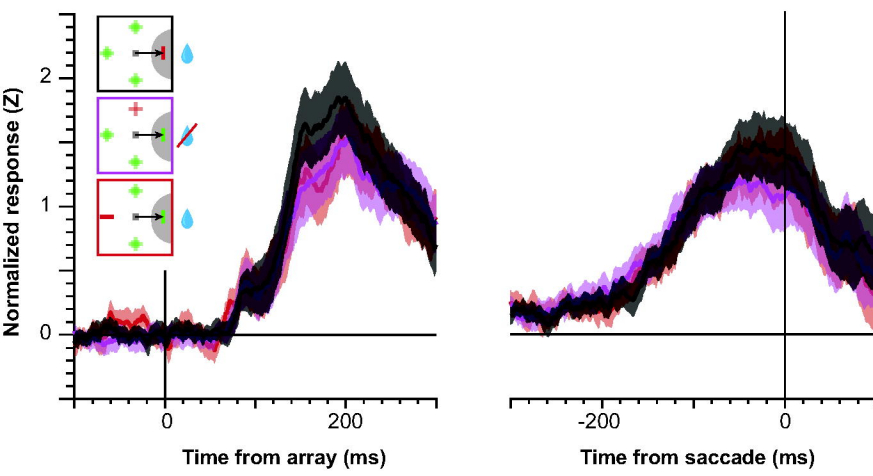


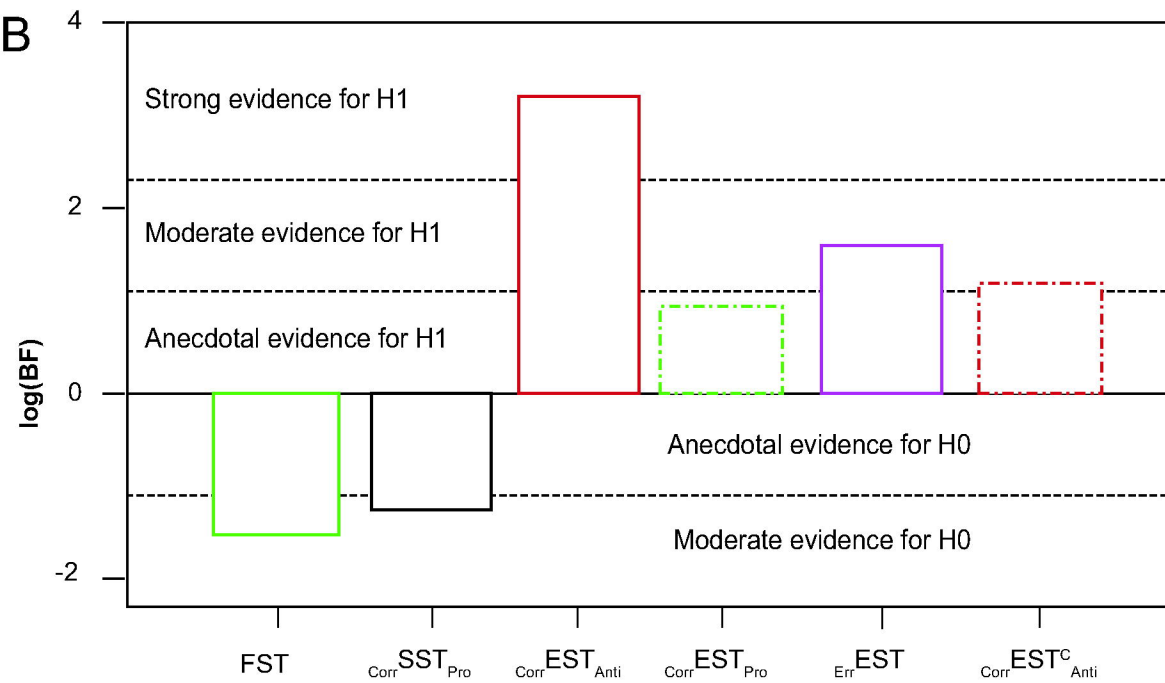
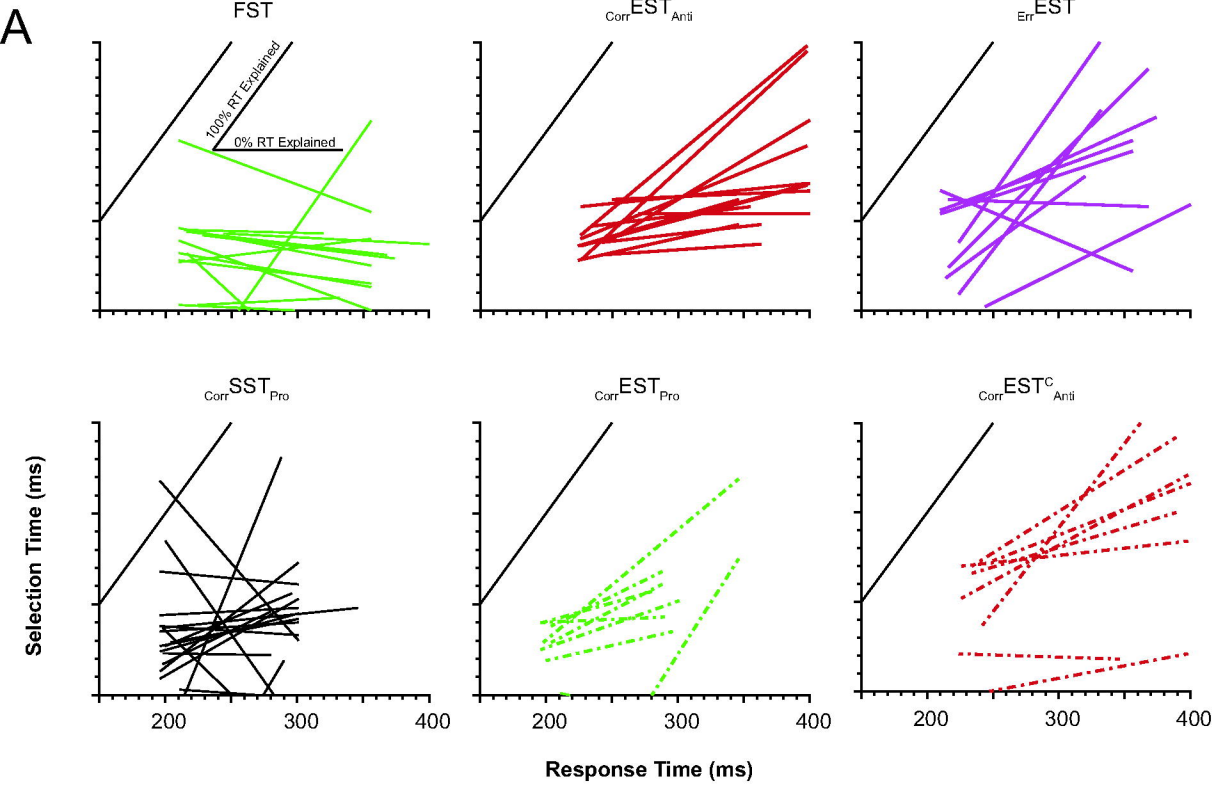


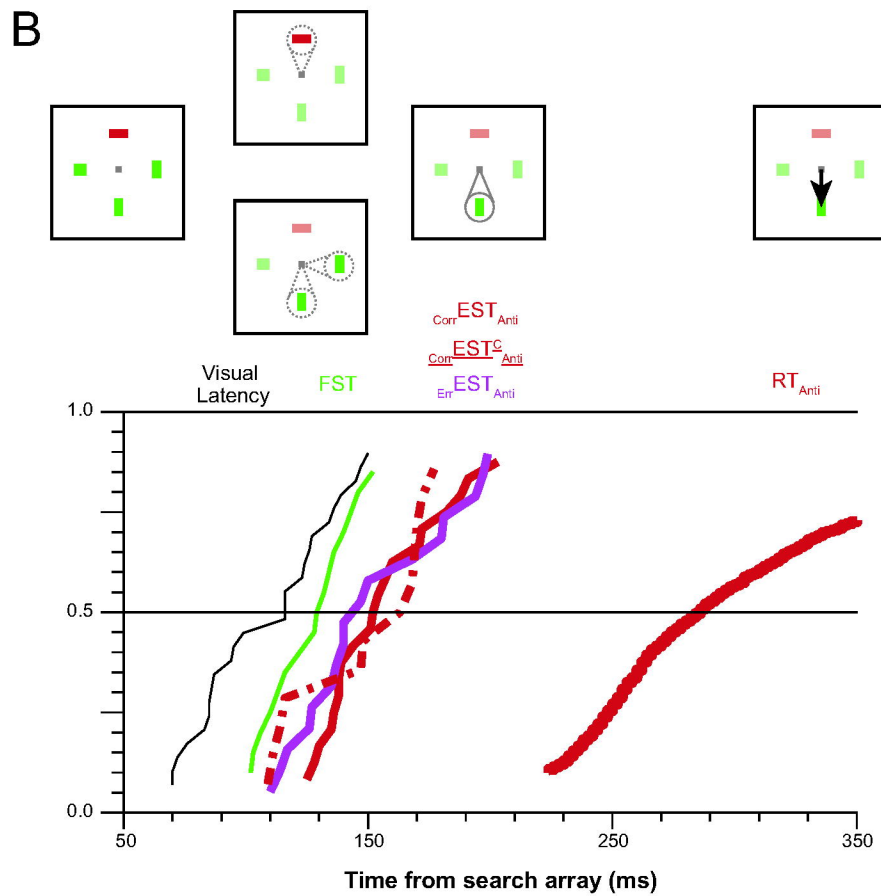
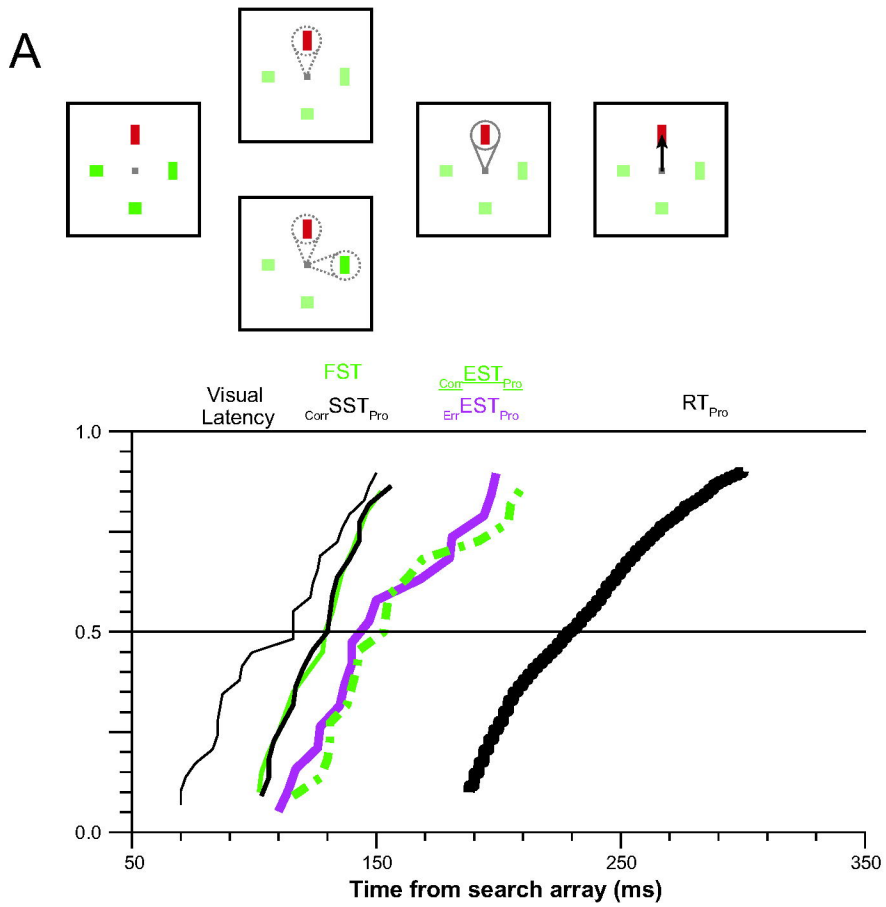












Low Schall Figure 10

Table 1

Measure	Mean \pm SEM (ms)	Mode (ms)	$p\left(\frac{\Delta \text{ Selection Time}}{\Delta \text{ Response Time}} > 0\right)$	BF
FST	130 \pm 30	134	0.683	0.22
CorrSST_{Pro}	136 \pm 37	137	0.377	0.28
CorrEST_{Anti}	160 \pm 34	134	0.002	24.62
CorrEST_{Pro}	154 \pm 51	133	0.027	2.55
ErrEST	155 \pm 41	133	0.011	5.64
CorrEST^C_{Anti}	149 \pm 57	168	0.021	3.29

Table 2

	FST	Corr ^{SST} _{Pro}	Corr ^{EST} _{Anti}	Corr ^{EST} _{Pro}	Err ^{EST}
Corr ^{SST} _{Pro}	$\chi^2(1,42) = 0.02, p = 0.888$				
Corr ^{EST} _{Anti}	$\chi^2(1,44) = 9.33, p = 0.002 *$	$\chi^2(1,46) = 8.35, p = 0.004 *$			
Corr ^{EST} _{Pro}	$\chi^2(1,42) = 5.58, p = 0.018 *$	$\chi^2(1,44) = 4.31, p = 0.038 *$	$\chi^2(1,46) = 0.01, p = 0.967$		
Err ^{EST}	$\chi^2(1,39) = 4.36, p = 0.037 *$	$\chi^2(1,41) = 3.56, p = 0.059 †$	$\chi^2(1,443) = 0.34, p = 0.560$	$\chi^2(1,41) = 0.20, p = 0.652$	
Corr ^{EST} _{Anti}	$\chi^2(1,34) = 3.90, p = 0.048 *$	$\chi^2(1,36) = 2.75, p = 0.097 †$	$\chi^2(1,38) = 0.24, p = 0.625$	$\chi^2(1,36) = 0.01, p = 0.905$	$\chi^2(1,33) = 0.03, p = 0.855$